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Multiple Interaction of Factors in the Distribution of Some Hawaiian Gelidiales (Rhodophyta)[1]

B. SANTELICES[2]

ABSTRACT: The biomass distribution of the three most common species of Gelidiales on three reefs of Oahu was found to form zones parallel to the shore correlated with the changing values of light intensity and water movement. *Pterocladia caerulescens* was restricted to the nearshore margin of reefs, tolerating intermediate intensities of water movement and some 30 to 100 percent of the incident light. *Gelidiella acerosa* occurred on the central part of the reefs, and while having similar light tolerances had a lower water movement optimum. Toward the seaward edge of the reef *P. capillacea* was restricted to areas with high water movement and much lower incident light (down to 6 percent). Thallus size and horizontal distribution of the two species of *Pterocladia* and biomass of all three species had a seasonal cycle with a maximum during December and a minium in May. All the biological cycles correlated significantly with seasonal changes in light intensity and water movement but did not relate to the seasonal changes of water temperature and salinity.

Laboratory experiments tested the effects of five single factors and nine types of interactions on the growth and bleaching of the three species of Gelidiales. Results indicate that water movement and light intensity are indeed the factors regulating growth and bleaching of these algae in the field. Salinity and temperature attained statistically significant effects only at values exceeding those found in the field. In all experiments water enrichment compensated for water movement as all three species attained maximum growth at comparatively lower water movement intensities when grown in fertilizer-enriched media. The enhancement of diffusion resulting in the laboratory from higher water movement, frequent water renewal or greater enrichment counteracted the bleaching effects of high light intensity and high temperature. This multiple interaction seems to have major ecological influence regulating pigment concentration, growth rate, and distribution of Hawaiian Gelidiales.

APART FROM TAXONOMIC and floristic studies (Abbott 1947, Loomis 1960, MacCaughey 1918, Neal 1930) little is known about the Hawaiian Gelidiales. Because they are sparse and form rather small turfs, they have not been specially considered in previous quantitative studies (DeWreede 1973, Doty 1971, Harger 1972, Santelices 1977*b*) of the Hawaiian benthic algae. Yet the Hawaiian shallow reefs with their restricted grazing pressure (Randall 1961) are quite appropiate for studying the interacting effects of several abiotic factors on the growth and distribution of these organisms.

Light intensity, rates of water movement, and temperature are the three most important environmental factors affecting the morphology and distribution of Gelidiales both in temperate and tropical latitudes (Santelices 1974). They tend to live in habitats with rather low light intensity (Dangeard 1966,

[1] Manuscript accepted 5 February 1978.

[2] University of Hawaii, Department of Botany, Honolulu, Hawaii 96822. Current address: Departamento de Biología Ambiental y de Poblaciones, Instituto de Ciencias Biológicas, Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.

Dellow and Cassie 1955, Hoek and Donze 1966, Kanda 1944, Seone-Camba 1964, 1965, Womersley and Edmonds 1958), and a few laboratory experiments (Chapman 1966, Ogata and Matsui 1965) have confirmed that they have lower photosynthetic saturation intensities than other intertidal algae. Some species are darker and larger under shaded conditions (Doty and Morrison 1954, Stewart 1968), while pigment destruction, stunted habit, and bleaching are common under intense sunlight (Seone-Camba 1965, Shepherd and Womersley 1970).

The Gelidiales are usually associated with strong wave action and rapidly moving waters (Hodgkins and Michel 1961, Hoek 1969, Lawson and Norton 1971, Primo 1953, Rao 1969, Shepherd and Womersley 1970, Tseng 1947). Water movement is known to affect benthic algae directly through its mechanical effect as well as indirectly by enhancing diffusion of gases and nutrients (Matsumoto 1959, Schumacher and Whitford 1965, Schwenke 1960, Vidaver 1972, Whitford and Kim 1966, Whitford and Schumacher 1961). These effects have such important ecological significance that each species of benthic algae has been suggested to have (Conover 1968) an upper and lower limit of water movement tolerance determined by diffusional requirements and mechanical resistance. Studies of such factors affecting the Gelidiales are lacking as yet, although it is known that nutrient additions to seawater lead to increased thallus length, weight, and nitrogen and phycoerythrin contents of some Gelidiales (Calabrese and Felicini 1970, Yamada 1961, 1964, 1967, 1972, Yamada and Iwahashi 1964, Yamada et al. 1964), which lead to larger and darker thalli similar to those sometimes found in habitats with low light intensity.

Studies of temperature effects on the Gelidiales have related this factor to their temporal distribution. Species presence (Conover 1958, Zaneveld and Barnes 1965); growth rates of individual thalli (Barilotti and Silverthorne 1972, Dixon 1963, Guzmán del Próo and de la Campa de Guzmán 1969, Johnstone and Feeney 1944); population fluctuations (Conover 1964, Matsuura 1958); tetraspore formation, shedding, and germination (Barilotti and Silverthorne 1972, Katada 1955, Katada et al. 1953, Seone-Camba 1965, 1966, Suto 1950); and agar content all vary seasonally and are apparently regulated by temperature changes. Most species reach maximum thallus size when the temperature is submaximum for the locality. The thalli then begin to bleach and start dying during the warmest periods at the end of the summer, the species persisting thereafter at reduced population densities. However, the field studies show that temperature is not necessarily the sole controlling factor since other seasonal parameters, such as light intensity and nutrients, have only rarely been taken into account.

The present research was undertaken to quantify biomass variations of the most important Gelidiales in Hawaii and to relate their patterns of variation to the interacting effects of environmental parameters. It was expected that the distribution of Hawaiian species would depend principally on degrees of light intensity and water movement or their combined effects. Since bleaching of culture-grown thalli can be prevented by nutrient additions, it was expected that the diffusional effects of increased water movement could prevent the bleaching effects of light intensity. Other environmental parameters were expected to be secondary or of comparatively little importance in Hawaii, where there are small ranges of annual variation (for example, in temperature). It was expected that, in addition to morphological differences, various species could be characterized by their physiological responses to light intensity and water movement and by different tolerance limits and optimum values for these two factors, as Conover (1968) has suggested.

MATERIALS AND METHODS

Field Studies

Three areas (Figure 1) were selected on the island of Oahu, Hawaii, for studies of the horizontal distribution of the three most

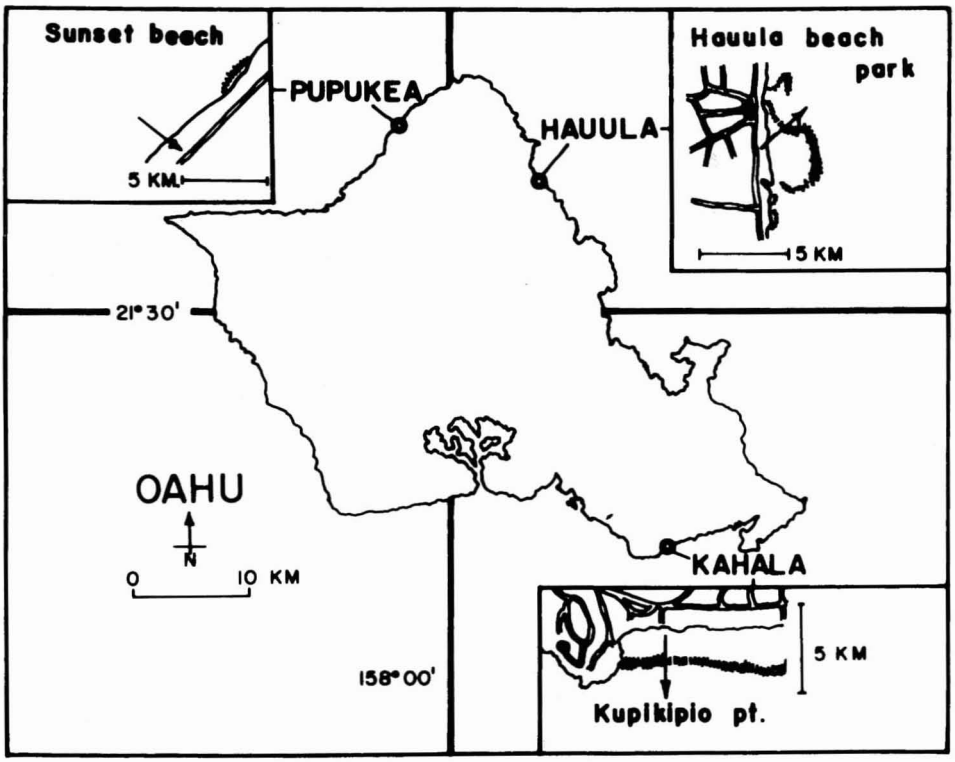

FIGURE 1. Map of the island of Oahu, Hawaii, showing the locations of the three sample sites. Arrows indicate the positions of the transects.

common species of Gelidiales, *Pterocladia caerulescens*, *Gelidiella acerosa*, and *P. capillacea* (see Santelices 1976*b*, 1977*a* for taxonomy). Each area had relatively homogeneous algal cover, easy access, and at least one of the species under study in sufficient numbers to maintain a 1-year sampling.

Two of the study areas, Hauula and Pupukea, are located on the windward (north to northeast) side of Oahu. The first is a reef flat about 10 meters to the left of the Hauula Beach Park, while the second is a small tunnel directly fronting Pupukea Beach Park. The third area is located on the south side of the island about 1 km south of Kahala Park. While both the Kahala and the Hauula study sites were shallow fringing reefs of variable offshore extension, the Pupukea study site was the floor and the short platform outside a natural tunnel known as Shark Cave.

At each locality a representative estimate of monthly changes in distribution, biomass, and fertility of the three selected species throughout the year was attempted. Sampling procedures were similar at the Hauula and Kahala reefs. A 5-meter-wide band running from the shore to the seaward edge of the reef was permanently laid out. Within this band a 20-cm-diameter steel ring was tossed at even distances across the reef. All the Gelidiales included in the sample were removed, placed in a numbered plastic bag, and brought to the laboratory. The size of the sampling ring (0.031 m^2) was judged adequate to allow fair representation of these algae and small enough to be sampled within a reasonable amount of time. The sample size was determined by applying the running mean technique (Kershaw 1964) to *Gelidiella acerosa*, which at that time was the most widespread and frequent species of Gelidiales on the reef. In total, about 20 samples, or 0.63 m^2 of the Kahala reef, and 15 samples, or 0.47 m^2 of the Hauula reef, had to be

sampled every month to give an adequate representation of the biomass of the species.

Sampling at the Pupukea site was originally similar to the above and included ten quadrats of 400 cm^2 each, placed on the reef every 50 cm along the transect. After October, however, the intensity of water movement impaired the visibility of the algae to be collected. All efforts were thereafter concentrated in mapping the limits of horizontal distribution of one of the species (*Pterocladia capillacea*) on a bimonthly basis. The sampling area at this locality corresponded to the reef platform just outside the inshore end of a natural tunnel, the seaward entry of which receives the full impact of the waves that move throughout the tunnel to the short platform outside. Whenever possible, a handful of thalli was collected at the inshore entry and at three sampling sites located 1 meter apart along the reef platform. At the same time, using a glass-bottomed box, the number of clumps of the species occurring within four 0.90 m^2 permanent quadrats were counted. These permanent quadrats were set up on the reef platform outside the tunnel at distances of 1, 2, 3, and 4 meters from the inshore entrance.

In the laboratory, the algae were washed with fresh water, sorted by species, weighed to the nearest milligram using a Mettler P160 balance, dried for 3 to 4 days at 60°C, and then dry weighed. Field data on biomass were extrapolated to grams per square meter for each sampling site, averaged to obtain monthly values, and correlated with the several environmental parameters measured in the field.

Salinity, water temperature, relative water movement (diffusion enhancement values), and incident radiation were measured monthly at each sample site as described in a previous study (Santelices 1977*b*). Also considered was surface water temperature measured every 3 days by the Fish and Wildlife Service at Koko Head, 10 km from Kahala.

Laboratory Studies

Thalli of *Pterocladia capillacea* for laboratory experiments came from Pupukea, while those of *P. caerulescens* and *G. acerosa* were from Kahala. Algae were transported in seawater and reached the laboratory within 2 hours, where they were cleaned, wet weighed, and placed inside glass dishes (Pyrex 3250) with 250 ml of filtered seawater. The dishes were placed in four environmental cabinets (Percival, Model 2E30) set at temperatures of 20 ± 1.5°C, 24 ± 1.5°C, 28 ± 1.5°C, and 32 ± 1.5°C, respectively. Incident illumination inside each chamber was provided by two Westinghouse 25W showcase bulbs and six Westinghouse cool-white fluorescent tubes producing a maximum illumination of 1200 ft-c at a distance of 18 cm from the light source. Layers of neutral-density cloth were used to decrease the illuminance values to 600, 300, 200, 100, and 50 ft-c. A 12:12 hr dark:light cycle was used in all experiments.

The normal culture medium was filtered seawater (35 ‰ saline) secured at the University of Hawaii Aquarium, Waikiki Beach, Honolulu. Salinities of 10, 20, and 30 ‰ were obtained by dilution of normal seawater with glass-distilled water; salinities of 40, 50, 60, and 80 ‰ were obtained by the addition of NaCl to the seawater. All salinity values were frequently checked during the experiments with a refractometer.

Growth chamber experiments were in still water. The effects of water movement were studied on five rotary shakers adapted to receive eight dishes (Pyrex 3250), each containing 250 ml of filtered seawater and a piece of experimental thallus attached to a pile of four to eight glass slides, which maintained the alga in a benthic situation. The shakers were set to move at 40, 80, 120, and 160 revolutions per minute (rpm) and were illuminated by four Westinghouse cool-white fluorescent tubes producing 400 ft-c of illumination. In some experiments, illumination was reduced to 50 ft-c and a motionless control was routinely used in all water-movement experiments.

The usual growth medium was plain seawater renewed every 6 days. In some experiments a higher fertilizer concentration was desired and the seawater was renewed more frequently (for example, every 3 days or every day) or enriched by the addition of 50 ppm

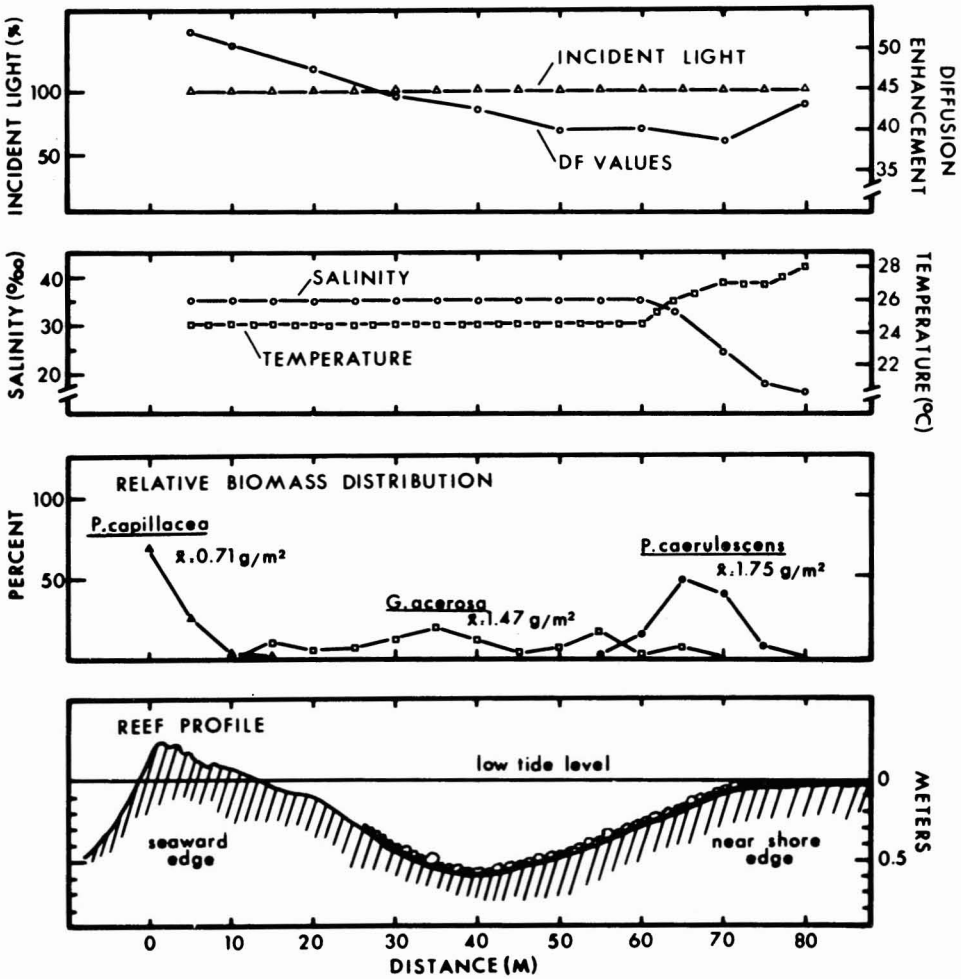

FIGURE 2. Climatological data and relative biomass distribution of three species of Gelidiales at Hauula in May 1973.

sodium nitrate. Diatoms were frequent epiphytes on the experimental thalli brought from the field and slightly contaminated most cultures. Since concentrations as low as 1 ppm of germanium dioxide proved toxic to *Pterocladia caerulescens*, diatom growth was reduced only by frequent cleaning of the culture vessels.

In total, five single factors—light intensity, temperature, salinity, water movement, and water quality—as well as nine types of interactions were tested. The simple and interacting effects of light intensity, temperature, and water quality were analyzed using three replicates, six levels of light, four levels of temperature, and three different manners of renewing or enriching the water. The main effects and interactions of light, water movement, and water quality were examined using four replicates, two levels of light, five levels of water movement, and five different changes of water quality. The combined effects of temperature and salinity were studied using five replicates, nine levels of salinity, and four levels of temperature.

All experiments lasted 30 days and results were evaluated using two different criteria: daily growth rates and relative bleaching. Growth rate was defined as increase in wet weight per unit of time, and bleaching as

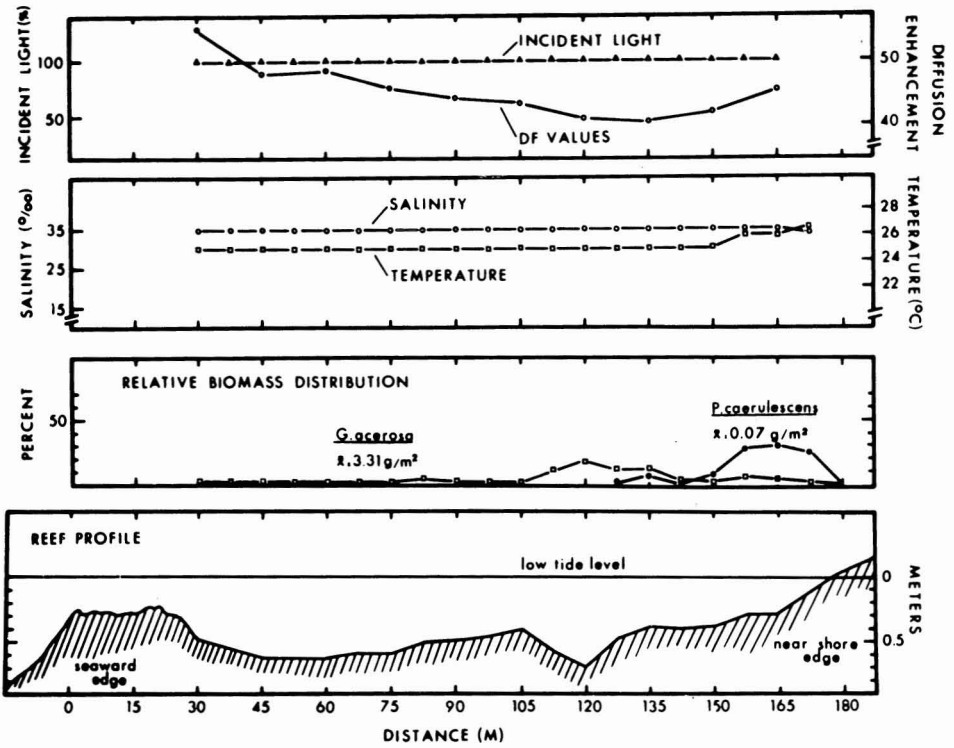

FIGURE 3. Climatological data and relative biomass distribution of two species of Gelidiales at Kahala in June 1973.

when a thallus had completely lost its pigmentation and had no mechanical resistance to slight efforts to dislodge it with a pair of forceps. Relative bleaching was measured by weighing the bleached portion of each thallus at each treatment.

RESULTS

Field Studies

HORIZONTAL BIOMASS DISTRIBUTION: The relative biomass distribution of *Pterocladia caerulescens*, *Gelidiella acerosa*, and *P. capillacea* (Figure 2) was quantified on the Hauula reef during preliminary surveys in May 1973. Hauula is a fringing reef whose shallow part extends about 80 meters offshore, ranging from +0.10 to −0.60 meter deep at low tide. It is fully exposed to direct sunlight and directly exposed to incoming waves. Most of the reef is paved by melobesioid algae interrupted by some boulders and sand near the shoreline. The average biomass of each species on the reef was 1.75 g dry/m^2 for *P. caerulescens*, 1.47 g dry/m^2 for *G. acerosa*, and 0.71 g dry/m^2 for *P. capillacea*. *Pterocladia caerulescens* appeared restricted to the nearshore edge of the reef, *P. capillacea* occurred in the seaward reef margin, and *G. acerosa* extended across the flat overlapping the two other species.

The values of water salinity and temperature measured at Hauula (Figure 2) are almost uniform (25°C and 35 ‰) across the reef and change only close to the shoreline during low tides. Diffusion enhancement values (DF) are low (38.30 to 42.50) across the central, deeper portion of the reef where *G. acerosa* is most abundant and rise at each margin where the two species of *Pterocladia* occur. The DF values are higher at the seaward edge of the reef (up to 50.70) than those close to the shoreline (43.40), as ex-

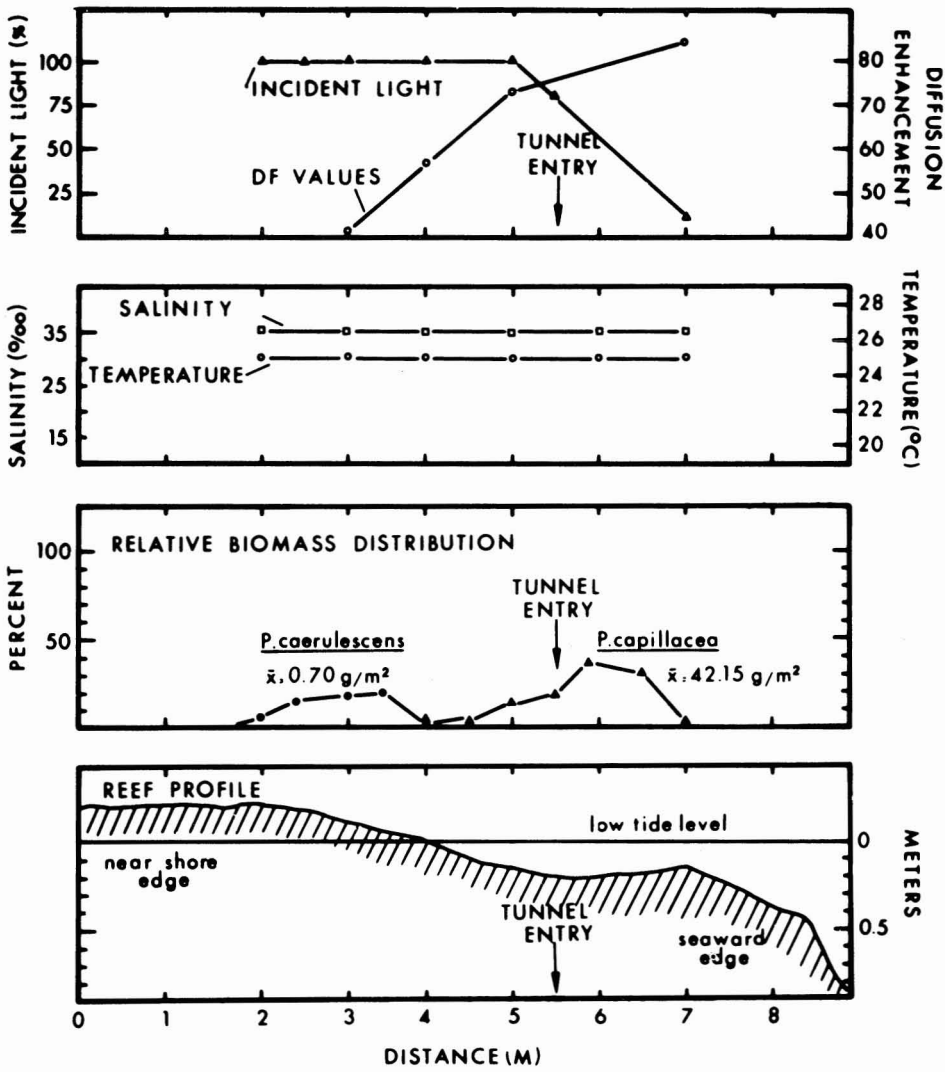

FIGURE 4. Climatological data and relative biomass distribution of two species of *Pterocladia* at Pupukea in August 1973.

pected for a reef directly exposed to the action of incoming waves. Values of incident light intensity are similar across all the reef flat, thus not correlating with the distribution of any of the species. However, all thalli exposed to full sunlight were bleached or appeared paler and smaller than those occurring under stones and boulders.

The patterns of distribution of species and physical parameters at the Kahala reef (Figure 3) are similar to those at Hauula. Kahala has a fringing reef extending about 300 meters offshore whose shallow portion ranges from −0.10 to −0.70 meter deep. There, *P. caerulescens*, with an average of 0.07 g dry/m^2, was also restricted to the nearshore edge and *G. acerosa*, with an average of 3.31 g dry/m^2, extended across most of the reef flat. The third species, *P. capillacea*, was not found at Kahala and it is uncertain whether it occurs further seaward. Detailed sampling of that edge was impossi-

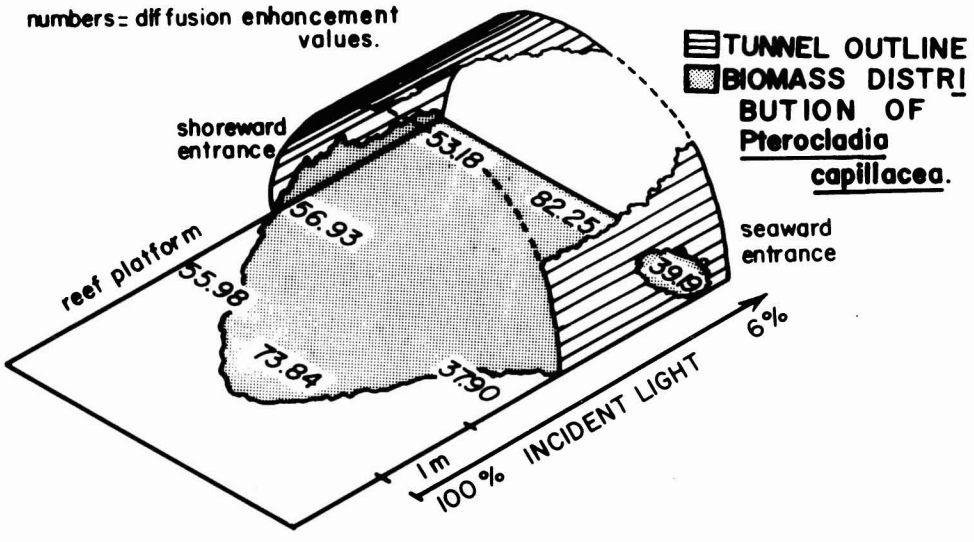

FIGURE 5. Distribution of *Pterocladia capillacea* at Pupukea in relation to water movement (as diffusion enhancement values) and light intensity.

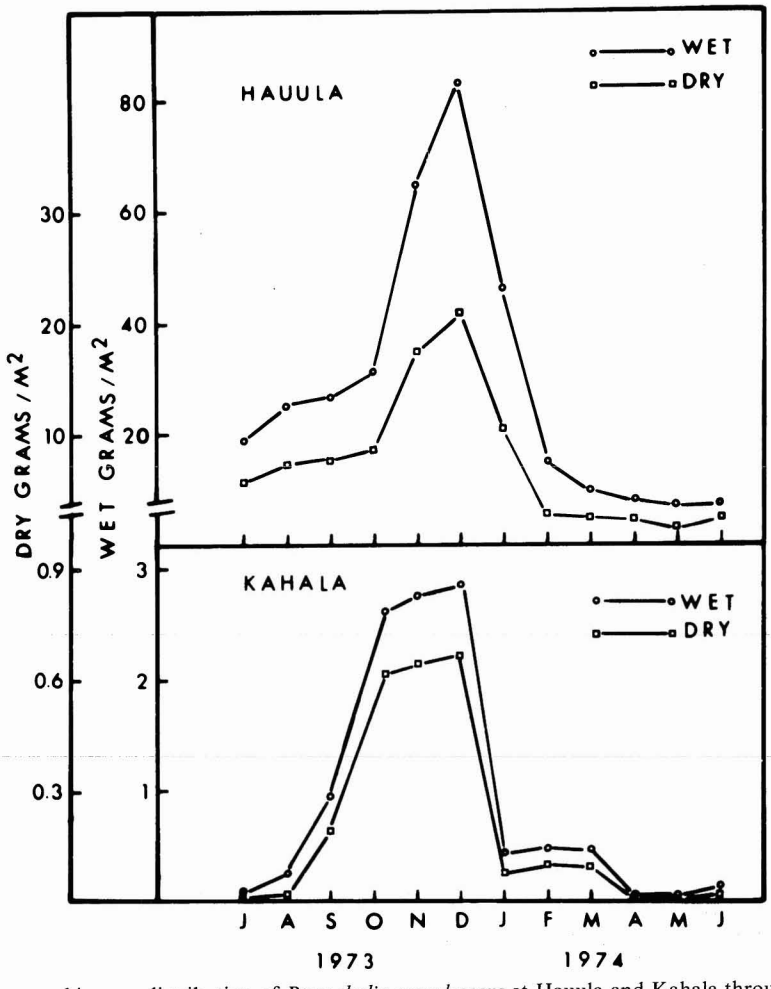

FIGURE 6. Average biomass distribution of *Pterocladia caerulescens* at Hauula and Kahala throughout the year.

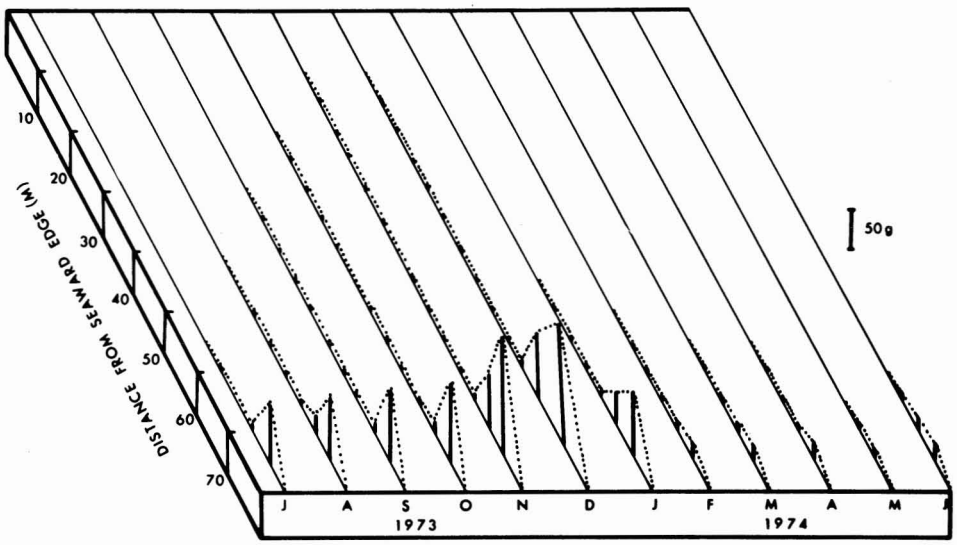

FIGURE 7. Temporal and spatial changes of biomass distribution (g dry/m^2) of *Pterocladia caerulescens* at Hauula.

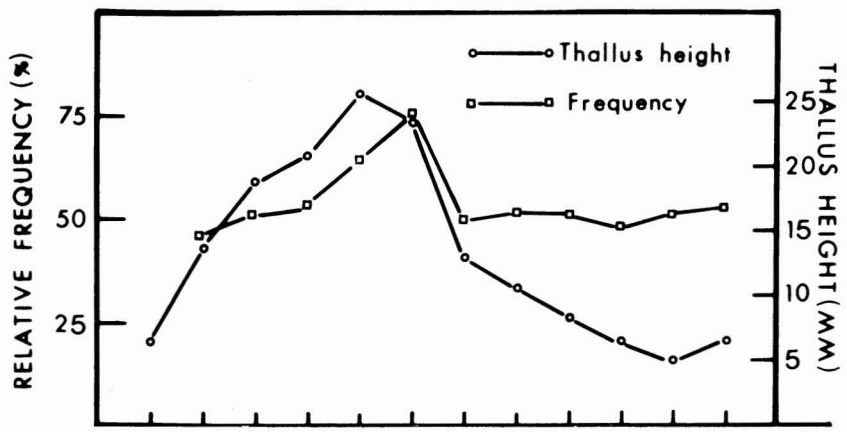

FIGURE 8. Annual changes in relative frequency and thallus length of *Pterocladia caerulescens* at Hauula.

ble due to strong wave action. Temperature and salinity variations across the reefs are restricted to areas close to the shoreline. Incident light remains constant across the reef, and diffusion enhancement values are lower (40.67) at the central portion of the reef, higher (45.48) toward the shoreline, and highest (55.98) close to the seaward margin.

The sample site at Pupukea (Figures 4, 5) extends about 10 meters in total length and ranges from -0.30 to $+0.30$ meter deep. Only the two species of *Pterocladia* (Figure 4) were found here, in a pattern of distribution analogous to that of the Hauula reef. *Pterocladia caerulescens* was mixed with other algae in the shoreward end of the platform, while the bulk of the biomass (close to 75 percent) of *P. capillacea* occurred inside the cave, extending only slightly into the platform outside. Salinity and temperature were evenly distributed, while incident light and water movement were uneven across the sampling area. The increasing DF values (up to 82.25) and the decreasing light intensities inside the cave (down to 8 percent incident light) correlated significantly ($r = 0.7216$ and

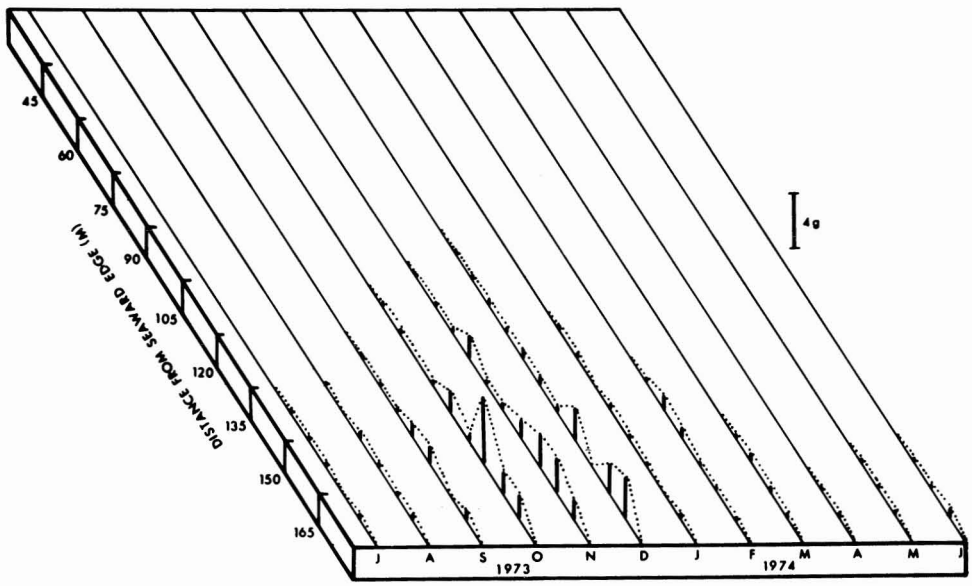

FIGURE 9. Temporal and spatial changes of biomass distribution (g dry/m^2) of *Pterocladia caerulescens* at Kahala.

−0.99783, respectively) with the biomass distribution of *P. capillacea*. This relationship was also evident if the total distribution of this species is mapped (Figure 5) in the sampling area. Inside the cave, where light intensity is reduced, the species occurred over a wide range of DF values that can be comparatively low (e.g., 39.19). Outside the cave, where the platform is exposed to 100 percent incident light, the species was absent from places with medium (e.g., 55.98, 45.80) and lower (37.90) water movement. Thallus bleaching was observed only on the parts of the platform without the protective ceiling of the cave.

SEASONAL CHANGES IN BIOMASS DISTRIBUTION: The maximum values of monthly average biomass of *Pterocladia caerulescens* occurred during December at the Hauula and Kahala reefs (Figures 6–8). The maximum value was almost 30 times higher at Hauula than at Kahala. Proportionately, however, the increase in biomass was earlier at Kahala, where in October the total biomass reached by the species was close to the annual maximum for that locality. The increased winter biomass of *P. caerulescens* at Hauula reflects its increase in distribution

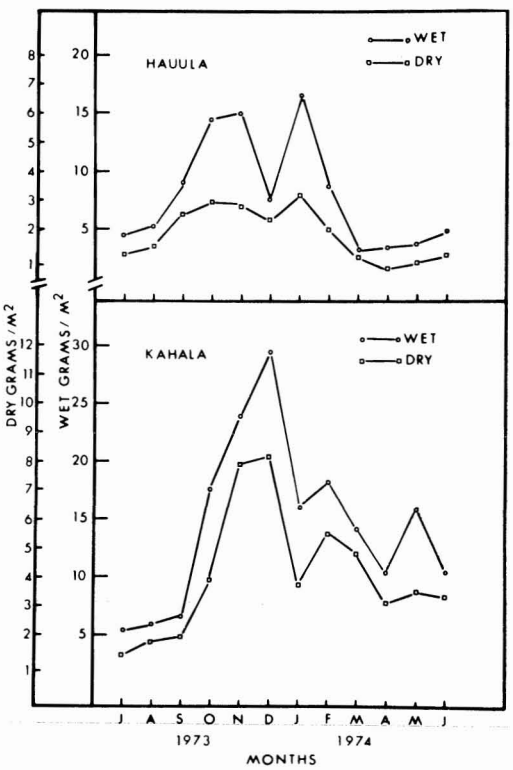

FIGURE 10. Average biomass distribution of *Gelidiella acerosa* at Hauula and Kahala throughout the year.

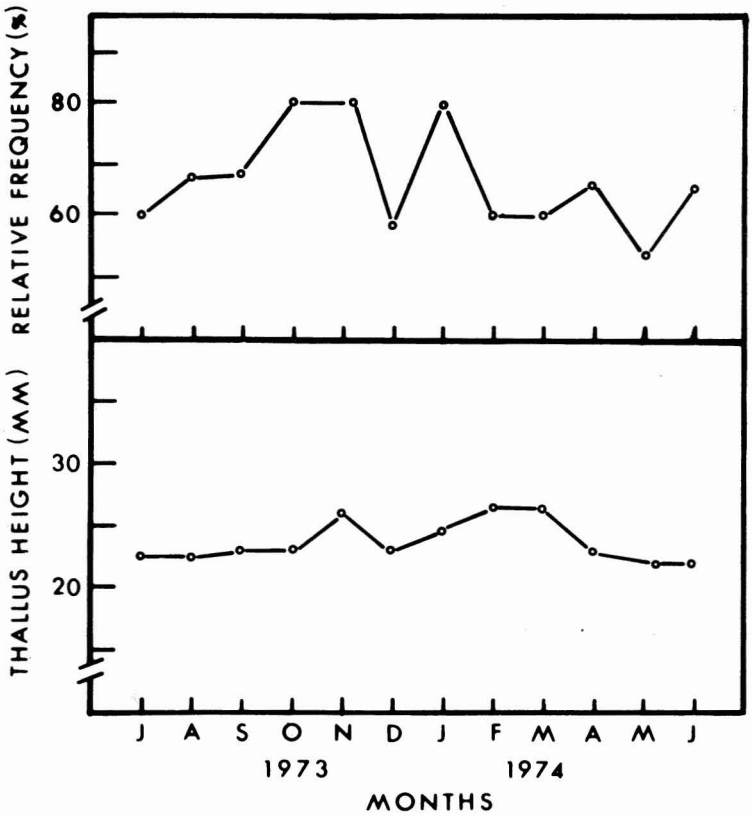

FIGURE 11. Annual changes in relative frequency and thallus length of *Gelidiella acerosa* at Hauula.

(and relative frequency; Figure 8) across the reef from the nearshore to the seaward margin (Figure 7). In addition, the average thallus length of the population (Figure 8) increases steadily during winter to a December maximum. At Kahala, a similar trend in biomass increase and horizontal distribution (Figure 9) was detected. After December, the biomass decreased at both localities and the species dissappeared from most of the reef other than nearshore. Thallus sizes also abruptly fell after January and remained almost unchanged until June.

Seasonal variations of biomass and horizontal distribution of *Gelidiella acerosa* at the Hauula and Kahala reefs are illustrated in Figures 10–13. The maximum monthly average biomass of *G. acerosa* occurs at different times at Hauula and at Kahala, and the seasonal curves have slightly different shapes. At Hauula, there was a steady increase in biomass from August to November. During December the biomass decreased. It increased again during January when it reached an annual maximum, and then steadily decreased and remained low from March to June. Changes in biomass correlate closely with the changes in frequency.

The maximum biomass of *Gelidiella acerosa* at Kahala (Figures 10, 13) is about twice that at Hauula and reaches its maximum during December. The pattern is similar to that at Hauula, but without a decrease in December. Bleaching of *G. acerosa* thalli in the field (Hauula) was measurable during December (1.68 percent of wet weight), March (9.7 percent), and April (0.3 percent). The occurrence of bleached thalli at the three times is coincident with decreases in thallus length, frequency, and biomass.

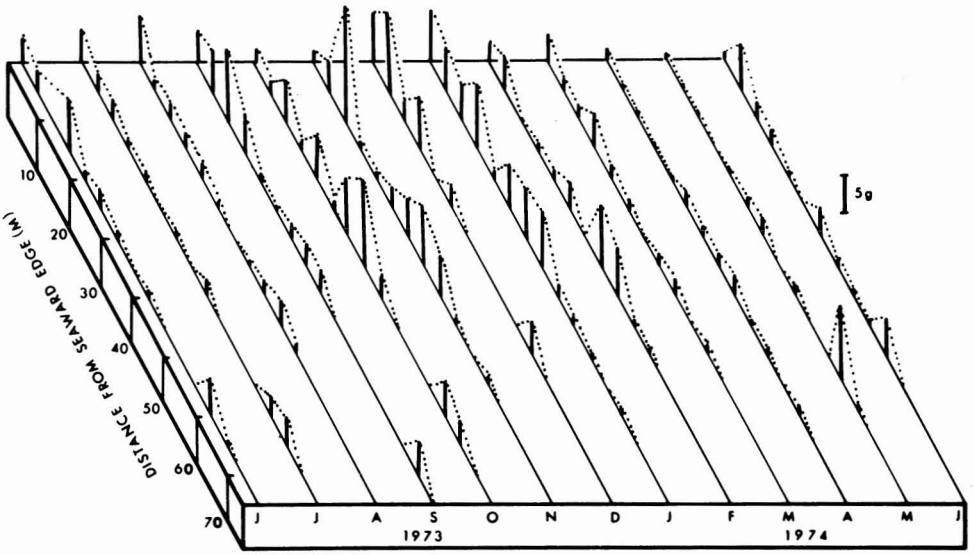

FIGURE 12. Temporal and spatial changes of biomass distribution (g dry/m²) of *Gelidiella acerosa* at Hauula.

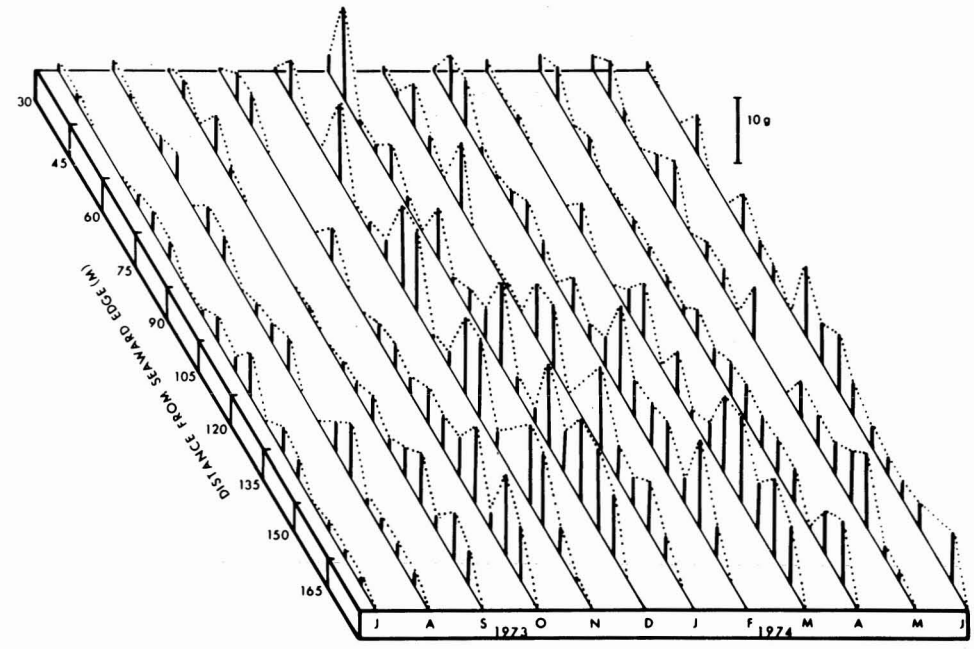

FIGURE 13. Temporal and spatial changes of biomass distribution (g dry/m²) of *Gelidiella acerosa* at Kahala.

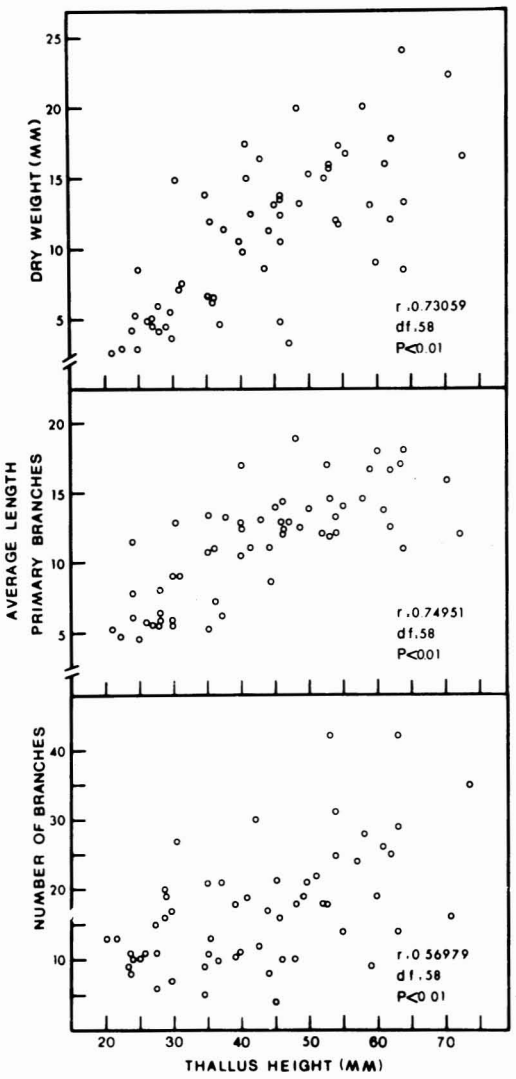

FIGURE 14. Dry weight, average length, and number of branches of *Pterocladia capillacea* as a function of thallus length.

Studies on seasonal variation of distribution and thallus length of *Pterocladia capillacea* were conducted at the Pupukea cave on a bimonthly basis. In this population the thallus length correlates (Figure 14) very closely with thallus dry weight because taller thalli have more and larger primary branches. Therefore, some insight into the changes in biomass could be obtained from the changes in thallus size combined with changes in distribution of the species throughout the year.

The horizontal distribution of *Pterocladia capillacea*, as measured by the number of thallus clumps occurring on the platform outside the cave (Figure 15), changes throughout the year. The species grew to a distance of 2 meters outside the cave mouth during August and October, extended to 3 meters in December and 4 meters in February, and remained at 4 meters until April. Thereafter, it retreated again to 2 meters. The number of clumps occurring at any sample site also changed during this time, steadily increasing through April and then decreasing. The number of clumps at or close to the cave entry was always larger than further outside, as was true of thallus length (Figure 16). At any sample site the thallus size was largest during December and February and smallest during June and August. Thalli growing at the cave entry or close to it were larger than those occurring further outside on the platform, regardless of season. Relative bleaching of *P. capillacea* (Figure 16) was measurable at almost all times. Close to the cave entrance bleaching was always lower than further outside, and it was significantly higher (up to 65 percent of all thalli) during June and August than during December (0–5 percent) and February. In general, the changes in relative bleaching correlated negatively with the changes in thallus length and distribution.

MEASUREMENT OF ENVIRONMENTAL PARAMETERS: Changes in monthly average solar radiation (cal/cm^2/day) on Oahu during the time of study are shown in Figure 17. Maximum radiation (up to 530 cal/cm^2/day) occurs between April and September and minimum (down to 300 cal/cm^2/day) during November, December, and January. Average radiation has a significant negative correlation with biomass distribution of *P. caerulescens* at Hauula ($r = -0.80584$) and at Kahala ($r = -0.60488$), with the thallus length of *P. capillacea* at Pupukea ($r = -0.58973$), and with the biomass distribution of *G. acerosa* at Hauula ($r = -0.67543$) and at Kahala ($r = -0.82733$).

Diffusion enhancement values measured by calcium sulfate blocks portray a seasonal

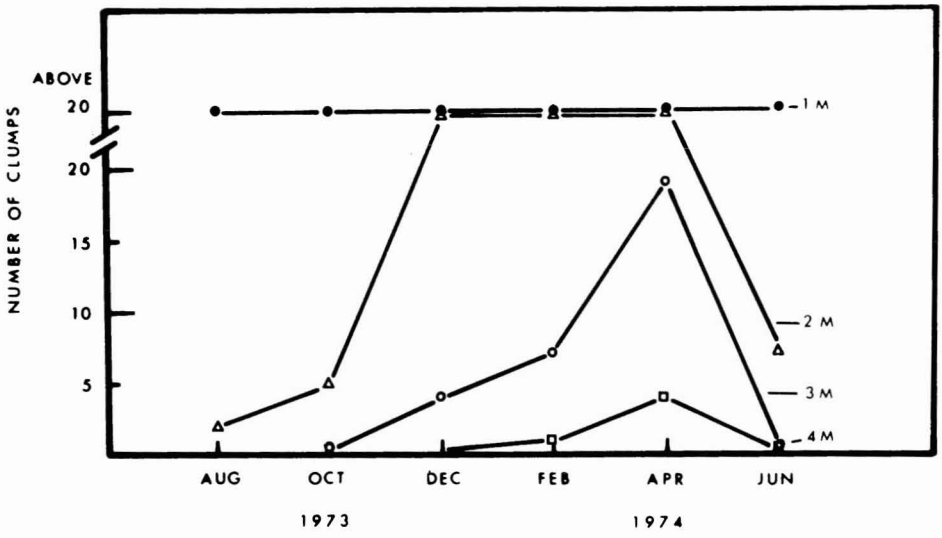

FIGURE 15. Annual changes in abundance (number of clumps per area) of *Pterocladia capillacea* on the platform outside the Shark Cave of Pupukea, at four distances from the inshore entrance.

cycle (Figure 17) at both Hauula and Kahala. On both reef flats the maximum monthly average for water movement occurred during November and reached a higher value ($\bar{x}$ = 69.92) at Hauula than at Kahala ($\bar{x}$ = 56.56). However, at Kahala the values reached a higher level relative to the maximum, comparatively earlier in the year, and for September the DF values were close to those found in November. Throughout the year, the DF values on both reefs (Figures 18, 19) were lower in the deeper, middle portions of the reef, higher close to the shoreline, and highest at the seaward reef edge. Therefore, the DF values for a given reef changed with horizontal distance, depth, and time of year. Average water movement has highly significant positive correlations with average biomass distribution of *P. caerulescens* at both reefs (r = 0.83126 and 0.81908) and for *G. acerosa* at Kahala (r = 0.76842).

At Pupukea, water movement values (Figure 17) were recorded during 5 of the 6 months of sampling. During December, the weather conditions were much rougher than during other months of the year and the calcium sulfate blocks were lost. It is thought that DF values for that month should be at least greater than those obtained in February, a month when four of the six calcium blocks were recovered. Throughout the year the level of water movement inside the cave was always higher than on the platforms outside. The monthly average DF values at Pupukea correlate significantly and positively with the changes in thallus length and distribution (r = 0.58432 and 0.64467) of *P. capillacea* in the Shark Cave.

Temperature variation between the two extremes of the reef in Hauula and Kahala at low tides are illustrated in Figure 20. The maximum yearly variation found in a whole reef was 4°C at Hauula and decreased to 2°C when only one edge of the reef was considered. Temperature variations at any one of the three localities do not follow a seasonal cycle that could correlate with changes in biomass of the species under study. The only seasonal change is the reduction in temperature differences between the two edges of the reef during the months of higher water movement.

The surface temperature data recorded off Koko Head are shown in Figure 20. The values show a seasonal cycle, varying about 2°C of maximum difference about 2 months after maximum average radiation; hence, they do not have significant correlation with the changes in biomass of the species under study.

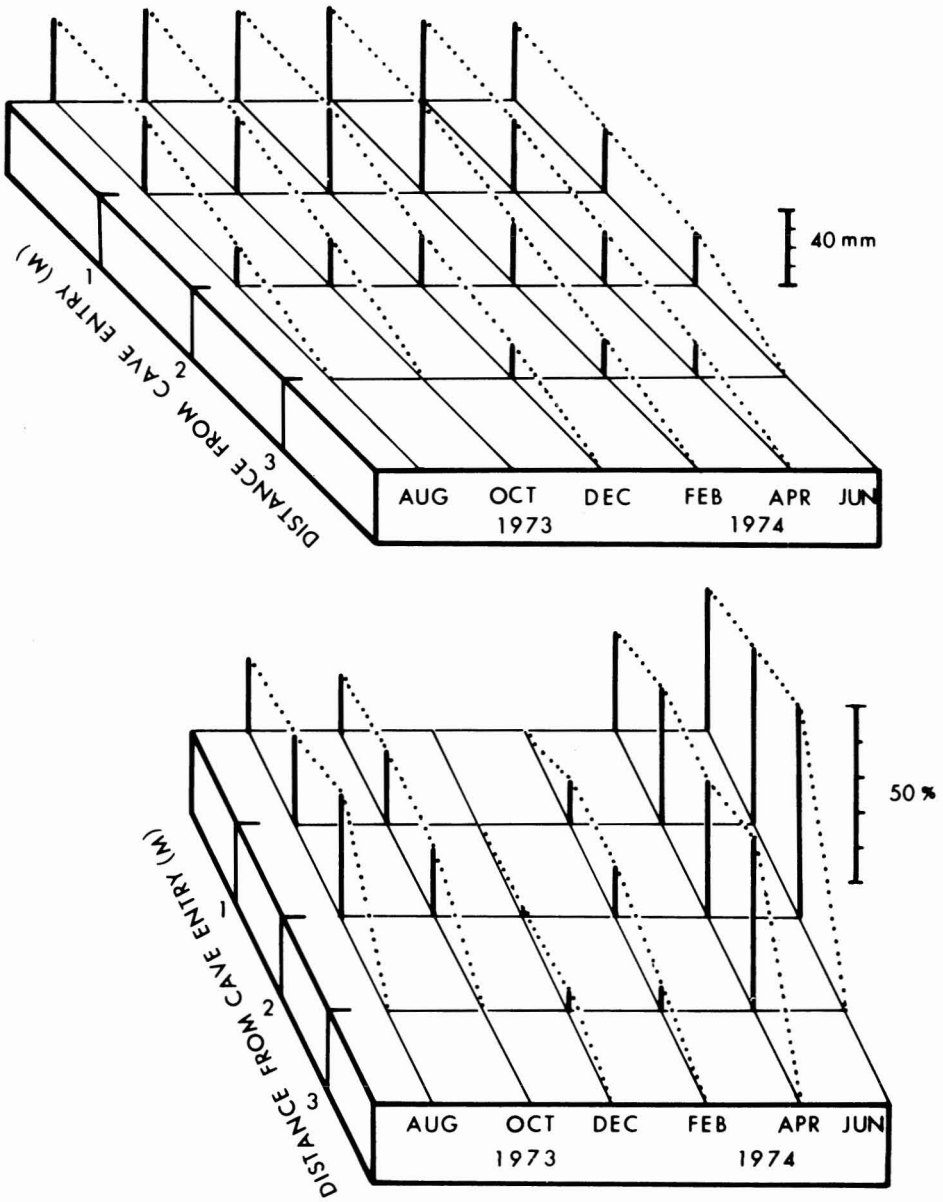

FIGURE 16. Annual changes in distribution, thallus length, and relative bleaching of *Pterocladia capillacea* on the platform outside the Shark Cave of Pupukea, at four distances from the inshore cave entrance.

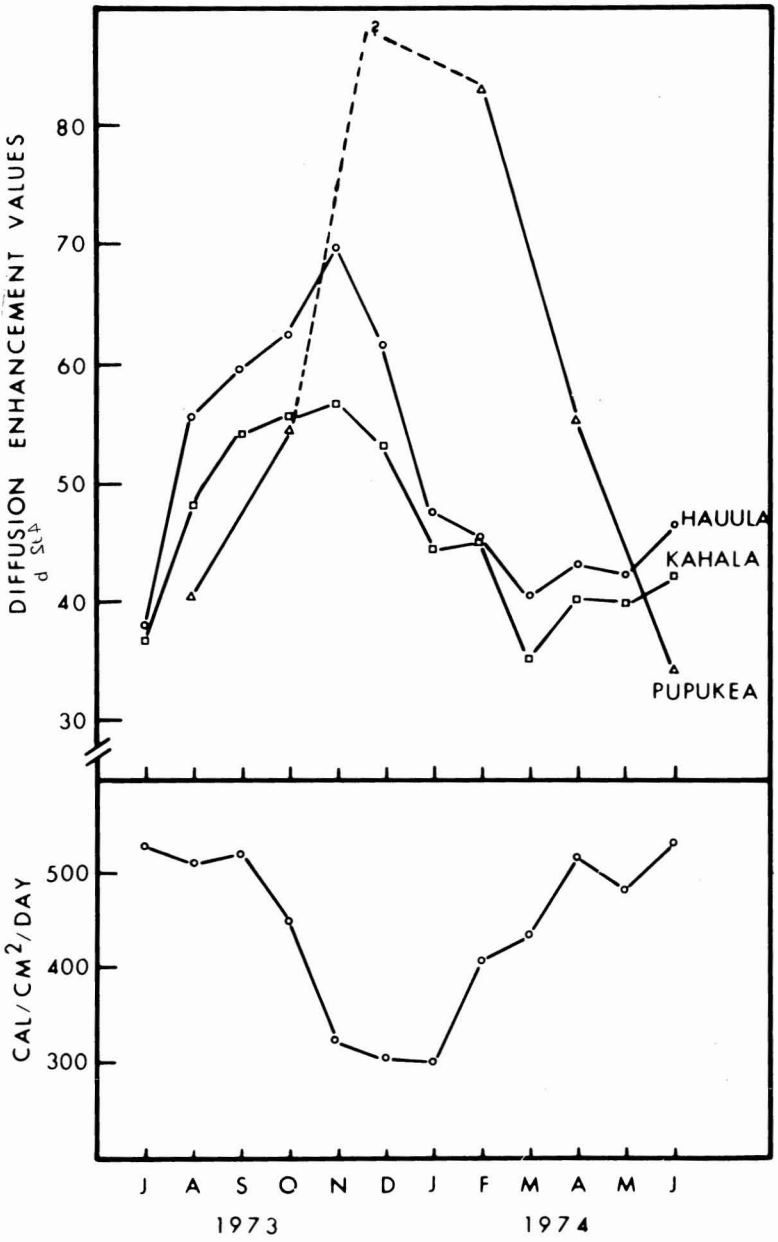

FIGURE 17. Annual changes in water movement and light intensity at three sites on Oahu.

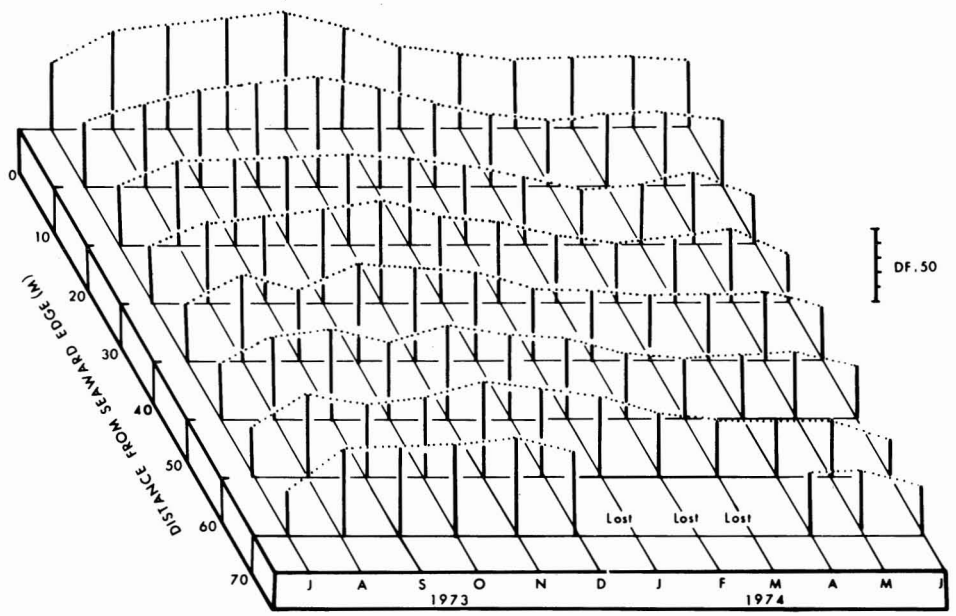

FIGURE 18. Temporal and spatial changes in diffusion enhancement values at Hauula.

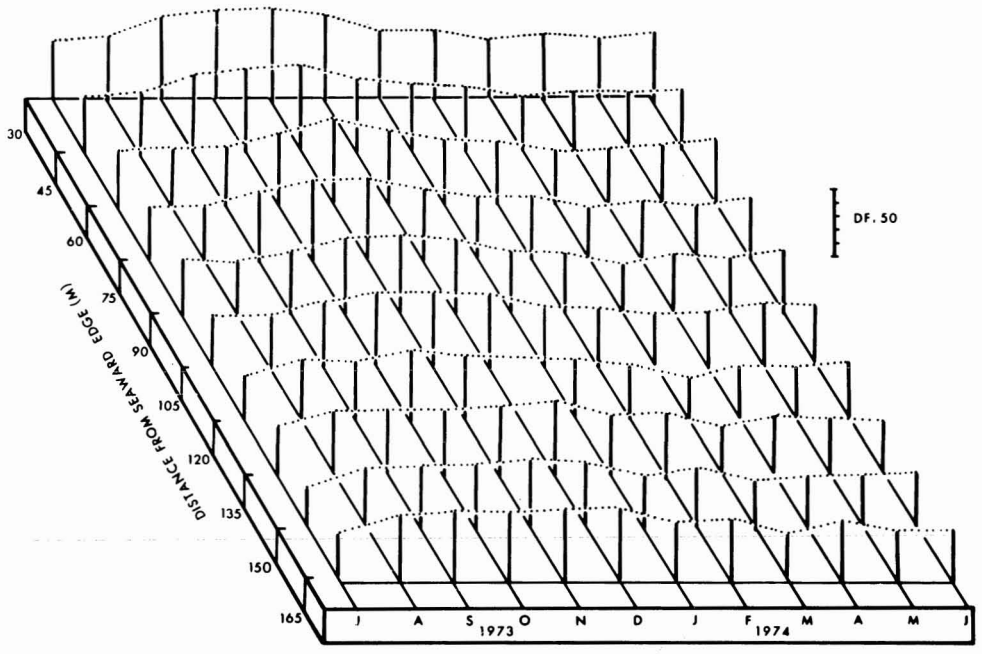

FIGURE 19. Temporal and spatial changes in diffusion enhancement values at Kahala.

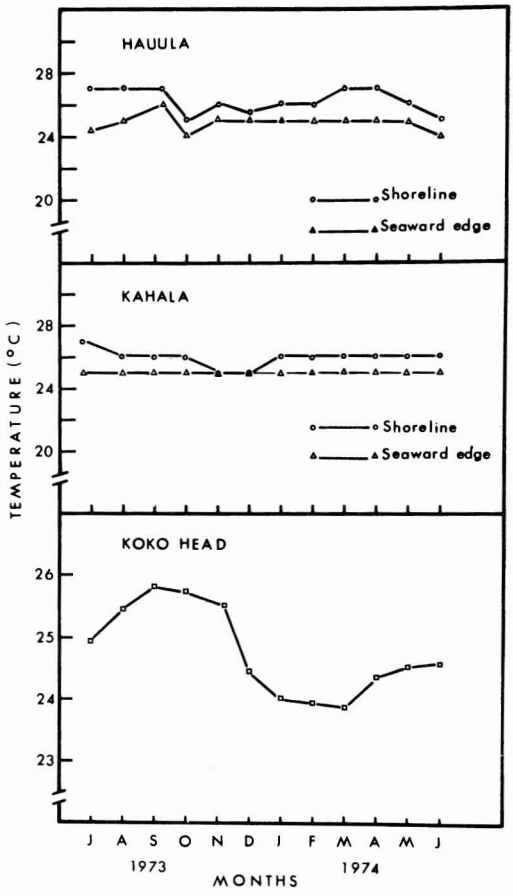

FIGURE 20. Annual changes in water temperature at the two edges of the Hauula reef, at the Kahala reef, and off Koko Head.

Changes in salinity at Hauula and Kahala (Figure 21) have a pattern somewhat similar to the temperature changes. Salinity is almost constant throughout the year at Pupukea, Kahala, and close to the seaward edge in Hauula, and during most of the winter at the shoreline of Hauula. It significantly decreases (down to 20 ‰) at low tides near the shoreline at Hauula during the months of less water movement, probably due to freshwater input from streams near the study area.

Laboratory Studies

Laboratory experiments tested the effects of light intensity, water quality, and temperature, and their interactions on the growth and bleaching of the three species of Gelidiales. The results are illustrated in Figures 22–24.

The daily growth rate and relative bleaching of *P. caerulescens* were significantly affected by all three environmental factors and several interactions that were tested (Table 1). In general (Figure 22), when the seawater is occasionally renewed (as every 6 days), the light saturation point is restricted to intensities as low as 200 to 700 ft-c, depending on temperature. The combination of high light (1200 ft-c) and high temperature (28 and 32°C) depresses the growth of the algae and produces intense bleaching. When water is renewed more frequently or when it is enriched with 50 ppm $NaNO_3$, bleaching is reduced and the light saturation point moves to higher light intensities, especially under high temperatures. Thus, the alga grows faster and reaches a maximum of almost 4 percent per day.

The results for *Gelidiella acerosa* are similar to those with the above species but differ in detail (Figure 23). All three factors and two interactions (Table 1) significantly affect the daily growth rate and relative bleaching of the species. At all temperatures (Figure 23) the light saturation point occurs between 300 and 600 ft-c and remains at that value with increasing frequency of seawater exchange. The addition of nitrates allows the alga to grow faster (up to 1.8 percent daily) at the two higher light and temperature combinations, but the results of almost all other 20 treatments remain unchanged.

The daily growth rate and relative bleaching of *P. capillacea* (Table 1) are also significantly affected (99 percent level) by the three main factors and by some of the interactions. When seawater is renewed every 6 days, the optimum light intensity for this species (Figure 24) is close to 200 ft-c regardless of temperature; above 300 ft-c there is depressed growth and extensive bleaching at any temperature tested. With increasing frequency of water exchange or with seawater enrichment, the optimum light intensity remains close to 200 ft-c, but bleaching is

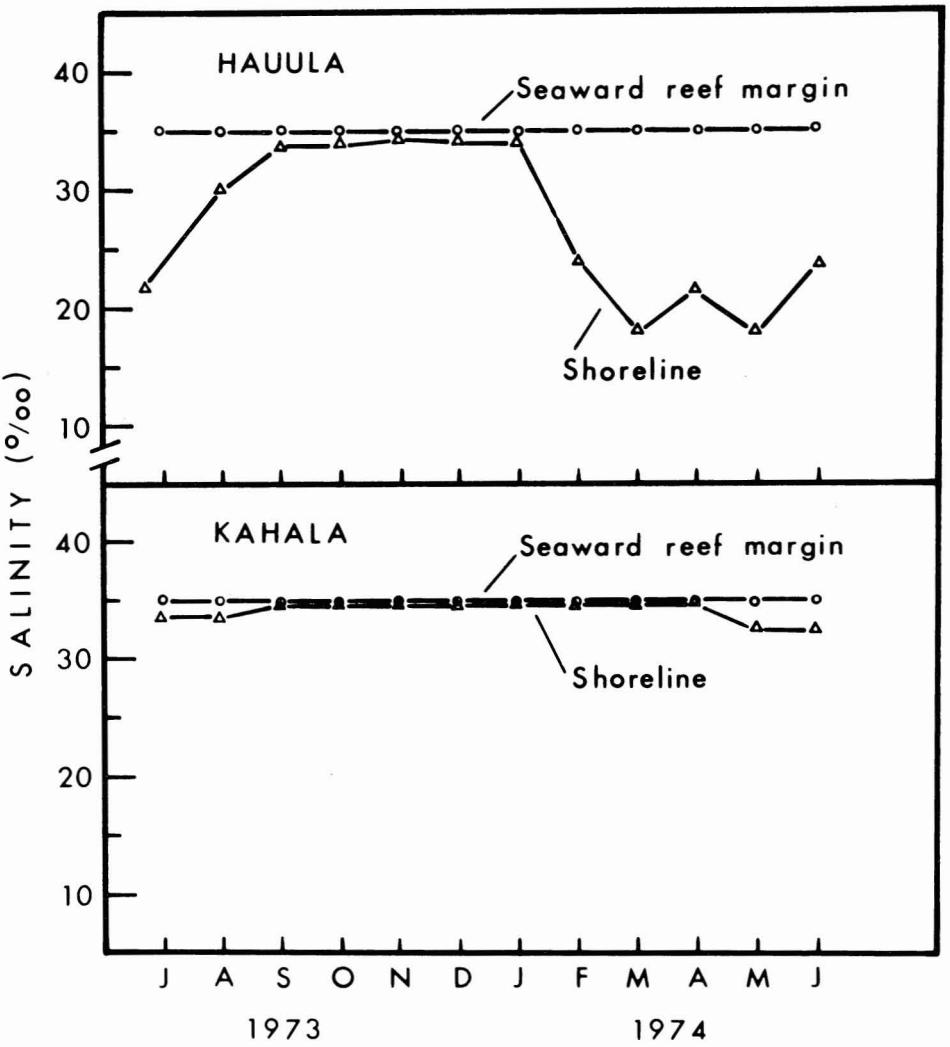

FIGURE 21. Annual changes in water salinity at the two edges of the Hauula and Kaha reefs.

reduced and the growth rates increase to a maximum of 3.5 percent per day.

A second type of experiment attempted to evaluate the role of light, water movement, water quality, and their interactions on the growth of the three species. Light intensities of 50 and 400 ft-c, rotary shaker velocities from 0 to 160 rpm, and as many as five different water quality treatments were used.

The daily growth rate of *Pterocladia caerulescens* (Figure 25, Table 2) was significantly affected (99 percent level) by the three main factors and by the two interactions, light–water movement and light–water quality. The growth rate under 50 ft-c is (Figure 25) low (close to 0.75 percent daily) and unaffected by changes in water movement or water quality. When the alga is grown under a higher light condition (400 ft-c), growth increases and the effects and interactions of the other two factors become evident. If seawater is changed infrequently (every 6 days), the optimum growth rate (1.9 percent per day) is reached at relatively high (120

TABLE 1

ANALYSIS OF VARIANCE AND SIGNIFICANCE VALUES FOR MAIN EFFECTS AND INTERACTIONS OF WATER QUALITY (WQ), LIGHT INTENSITY (LI), AND TEMPERATURE (T) ON THE GROWTH AND RELATIVE BLEACHING OF THREE SPECIES OF GELIDIALES IN HAWAII

		Pterocladia caerulescens				*Gelidiella acerosa*				*Pterocladia capillacea*			
		Daily growth		Relative bleaching		Daily growth		Relative bleaching		Daily growth		Relative bleaching	
SOURCE OF VARIATION	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Main plots													
WQ	2	8.31	<0.05	293.87	<0.005	7.81	<0.05	18.09	<0.02	72.34	<0.005	115.94	<0.005
Error	4												
Subplots													
T	3	35.95	<0.005	115.21	<0.005	10.57	<0.005	56.89	<0.005	141.74	<0.005	62.39	<0.005
T × WQ	6	1.70	0.12	18.79	<0.005	0.43	>0.25	2.27	0.14	10.49	<0.005	10.55	<0.005
Error	18												
Subsubplots													
LI	5	44.03	<0.005	249.50	<0.005	52.40	<0.005	60.13	<0.005	24.76	<0.005	129.83	<0.005
WQ × LI	10	2.25	0.025	47.51	<0.005	1.32	>0.20	1.17	>0.25	1.08	>0.25	0.34	>0.25
T × LI	15	4.30	<0.005	10.54	<0.005	2.79	<0.005	3.72	<0.005	6.45	<0.005	7.56	<0.005
WQ × LI × T	30	0.77	>0.25	3.34	<0.005	0.60	>0.25	0.56	>0.25	1.41	0.10	1.08	>0.25
Error	120												

TABLE 2

ANALYSIS OF VARIANCE AND SIGNIFICANCE VALUES FOR MAIN EFFECTS AND INTERACTIONS OF LIGHT INTENSITY (LI), WATER QUALITY (WQ), AND WATER MOVEMENT (WM) ON THE GROWTH OF THREE SPECIES OF GELIDIALES IN HAWAII

	Pterocladia caerulescens			*Gelidiella acerosa*			*Pterocladia capillacea*		
SOURCE OF VARIATION	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Main plots									
WQ	4	25.71	<0.005	2	1.70	>0.25	1	42.60	0.007
Error	12			6			3		
Subplots									
LI	1	385.40	<0.005	1	425.96	<0.005	1	151.65	<0.005
WQ × LI	4	9.67	<0.005	2	0.56	>0.25	1	11.37	0.017
Error	15			9			6		
Subsubplots									
WM	4	31.26	<0.005	4	9.64	<0.005	4	13.64	<0.005
WM × LI	4	9.04	<0.005	4	1.71	0.20	4	1.92	0.21
WM × WQ	16	1.11	>0.25	8	0.98	>0.25	4	0.79	>0.25
WM × WQ × LI	16	1.32	0.11	8	1.08	>0.25	4	0.36	>0.25
Error	120			72			48		

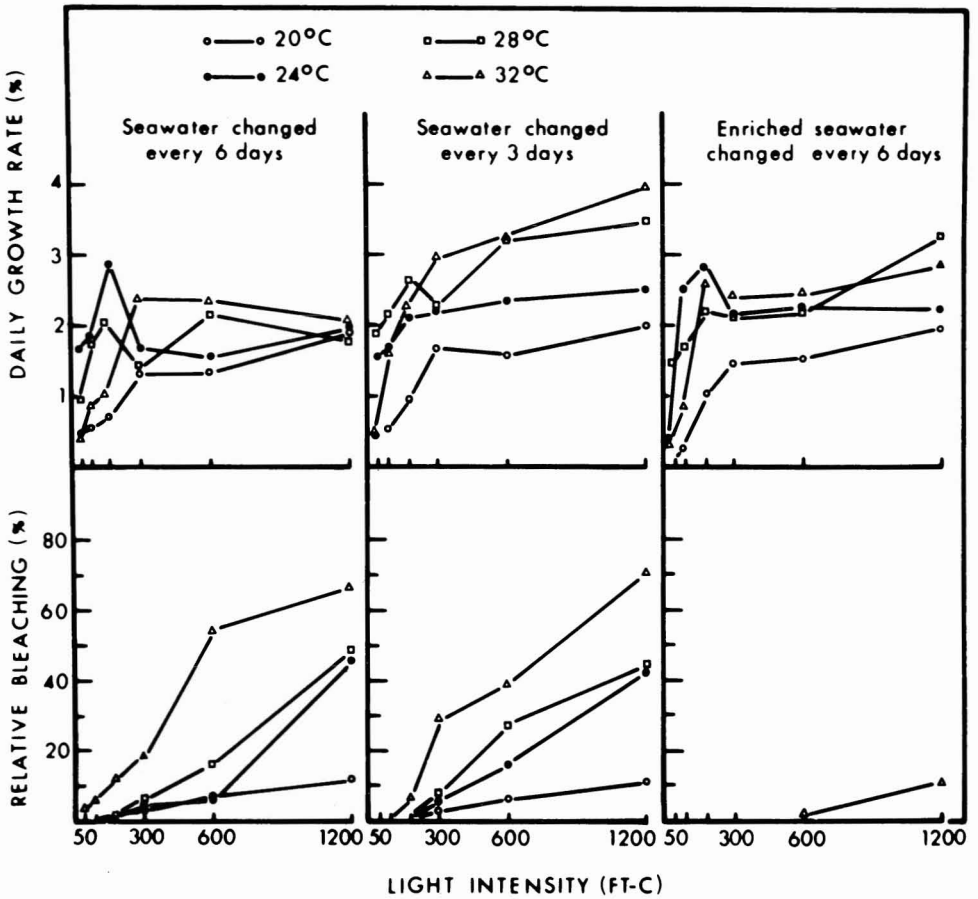

FIGURE 22. Daily growth rates and relative bleaching of *Pterocladia caerulescens* as functions of light intensity, temperature, and water quality.

rpm) levels of water movement, and significant differences between the growth achieved at the lowest (0 rpm), lower (40 and 80 rpm), and higher (120 and 160 rpm) water movement values are evident. When water is changed or enriched more frequently, the optimum growth is reached at lower (80 rpm) water movement values and the differences between 0 and 160 rpm are not significant.

Although the daily growth rate of *Gelidiella acerosa* (Table 2) is affected at a significant level (99 percent) only by light and water movement, this species shows (Figure 25) a pattern of response similar to that of *P. caerulescens*. No significant differences in growth result from any water movement level or enrichment when the species grows under 50 ft-c. When illumination is raised to 400 ft-c, differences in water movement levels become significant if unenriched seawater is infrequently changed. Enriching or exchanging water every day compensates for water movement as the growth achieved at the several water movement velocities are statistically similar. Proportionally, *G. acerosa* grows slower than *P. caerulescens* and as in that species some depression of growth occurs in several treatments at the highest water movement value.

The growth rate of *Pterocladia capillacea* (Figure 25) follows a pattern similar to the other two species but with specific differences.

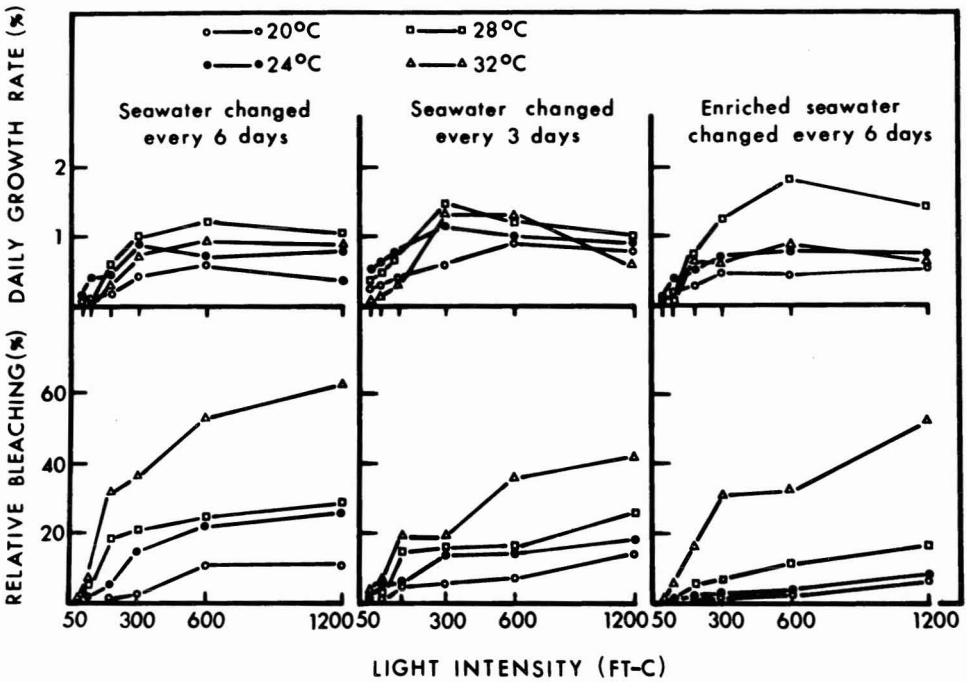

FIGURE 23. Daily growth rates and relative bleaching of *Gelidiella acerosa* as functions of light intensity, temperature, and water quality.

The three main factors and the interaction light–water quality are significant at the 99 percent level. In comparison with *P. caerulescens* and *G. acerosa*, the growth rate of this species at the lower (50 ft-c) light intensity is relatively high as the growth rates obtained at the lower and higher levels of water movement with unenriched seawater are significantly different at low illumination. At higher light intensity levels (400 ft-c) the growth rate increased significantly up to a maximum close to 4 percent daily when enriched seawater was used. Growth of the alga in enriched seawater is higher at any water movement (including 0 rpm) than the growth rates obtained at 160 rpm with plain seawater. Thus, enrichment compensates for the effects of water movement in the growth of this species also. Comparing the growth of this alga in plain seawater, both at 50 and 400 ft-c, no significant differences occurred between the various levels of water movement and light intensity, or their interactions. It is likely that the unenriched seawater is acting as a limiting factor under that condition. Thus, *P. capillacea* appears to have higher requirements of water exchange than the other two species.

A third type of experiment (Figure 26) studied the combined effects of temperature and salinity on the daily growth rate of the three species. Tolerance to a salinity range from 20 to 60 ‰ occurs at all temperatures tested for *Pterocladia caerulescens*, but the optimum values for growth change as a function of temperature. By contrast, the limits of tolerance of *Gelidiella acerosa* vary with temperature although the optimum for growth remains constant. Salinity tolerance limits are wider (10 to 80 ‰) at 24 and 28°C, while optimum growth occurs between 35 and 40 ‰ regardless of the levels of temperature tested. In the case of *P. capillacea*, both the tolerance limits and the optimum growth values are affected by temperature. The species can grow from 10 to 50 ‰ at 20°C and up to 80 ‰ at 28 and 32°C. The tolerance limits of all three species

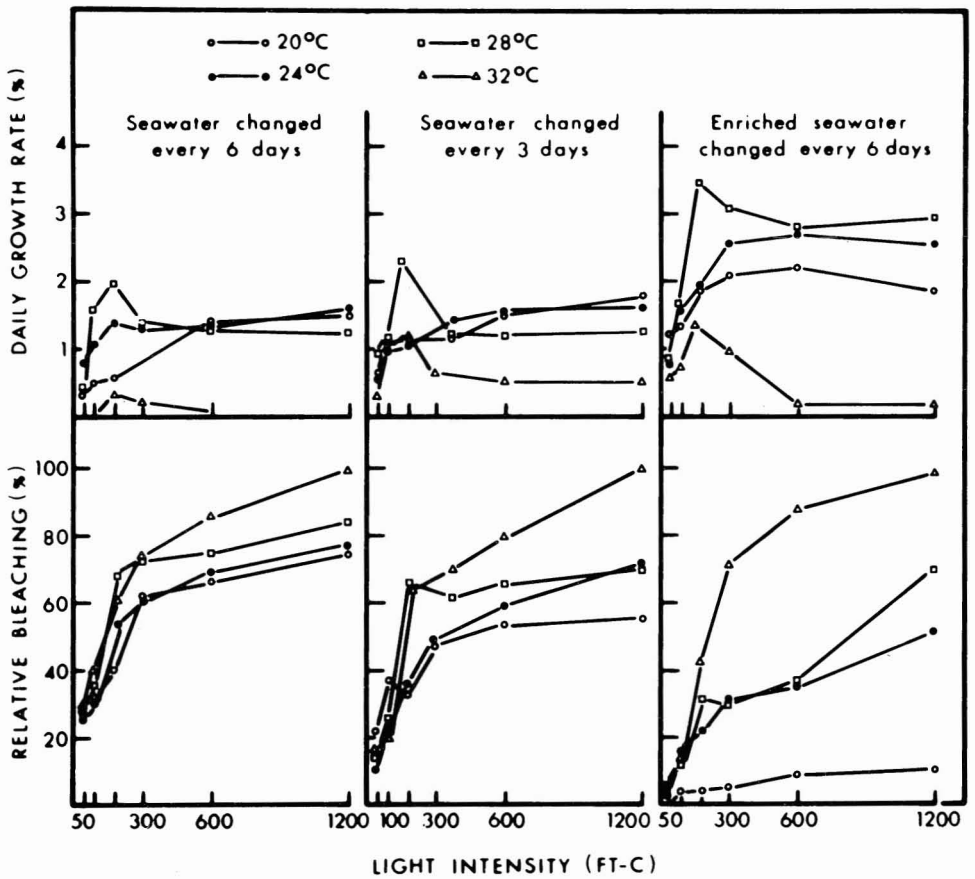

FIGURE 24. Daily growth rates and relative bleaching of *Pterocladia capillacea* as functions of light intensity, temperature, and water quality.

widely exceed the salinity variation recorded in the field.

DISCUSSION AND CONCLUSIONS

Most of the field and experimental work carried out in this research indicates that specific differences in tolerance ranges and optima of levels of light intensity, water movement, and their combined effects are the most probable causes of the observed distributions of Hawaiian Gelidiales. Temperature and salinity produce significant effects only at experimental values exceeding those found in the field.

As expected from the literature, the three species of Gelidiales had low light saturation values and their thalli appeared pale or bleached when exposed to full sunlight. Within this general pattern, however, there were specific differences. Full sunlight could be tolerated by *Gelidiella acerosa* and *Pterocladia caerulescens*, but was generally detrimental to *P. capillacea*. Likewise, the former two species had higher saturation intensities in laboratory cultures than *P. capillacea*.

Water movement also affects growth and distribution of these species. In the field, the highest water movement values were optimal for *P. capillacea*, but limiting for *P. caerulescens* and *G. acerosa*. In the laboratory, the highest experimental water movement values depressed growth in these last two species. The phenomenon is consistent with Conover's (1968) hypothesis that there is an

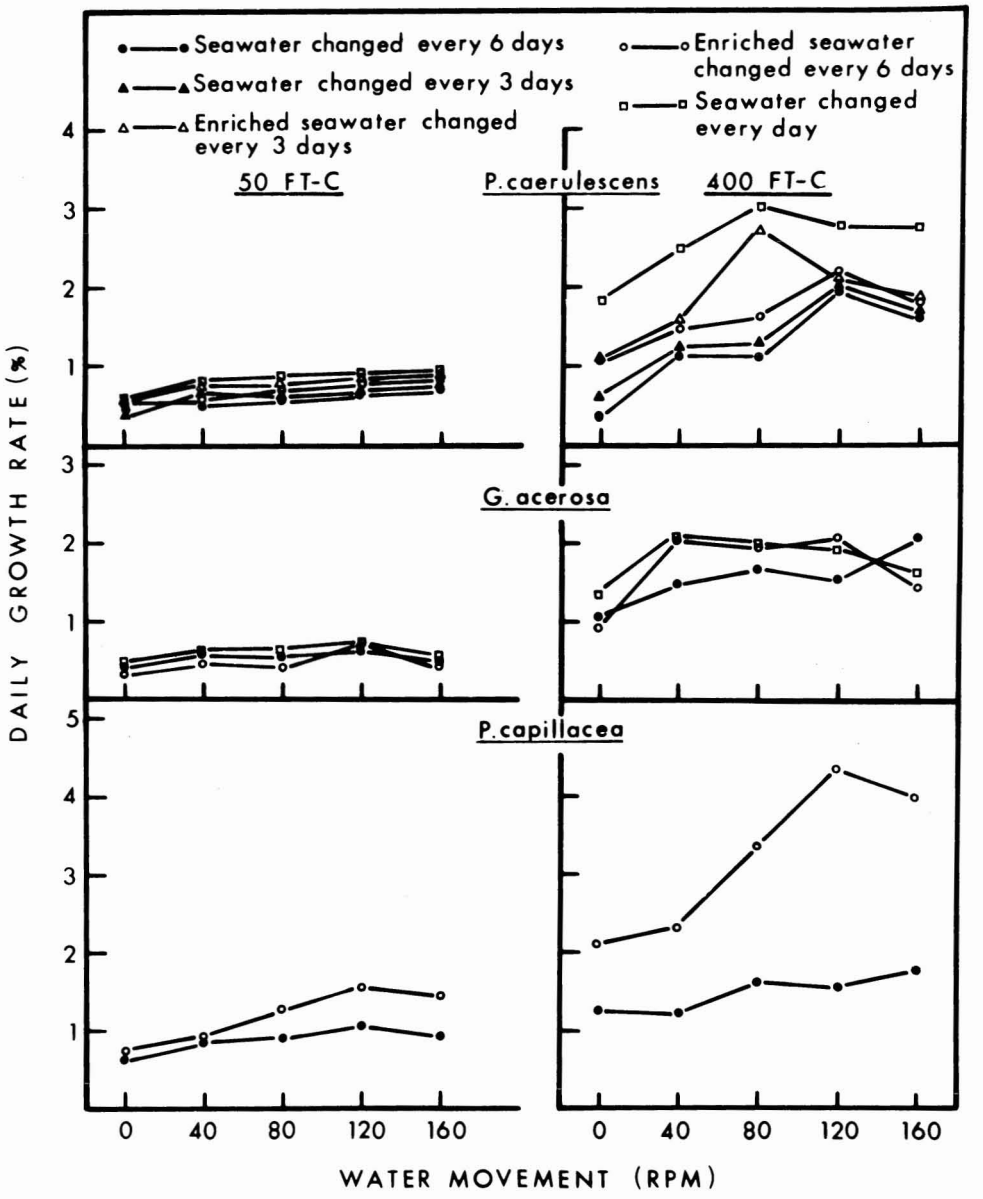

FIGURE 25. Daily growth rates of three species of Gelidiales as functions of light intensity, water movement, and water quality.

upper and lower current tolerance level for each algal species.

The experimental results show the close relationship between water movement, diffusion, and algal growth. Whenever seawater was infrequently changed or not enriched, there were significant differences in the growth achieved at the lowest and optimum water movement values. In addition, all three species attained maximum growth at relatively high water movement values. When the seawater was renewed every day, the differences in growth rates reached at several water movement values were not significant

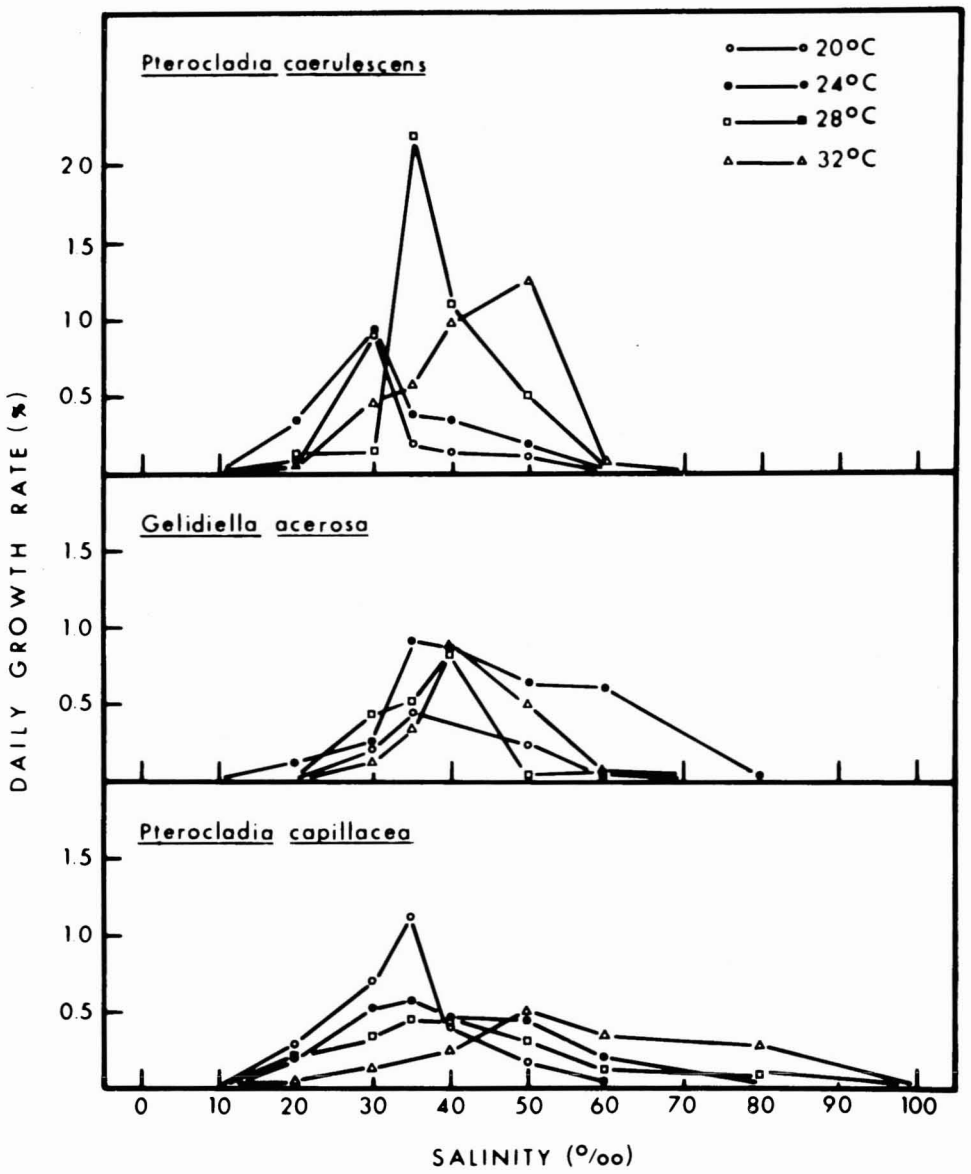

FIGURE 26. Daily growth rates of three species of Gelidiales as functions of salinity and temperature.

and maximum growth of each species was reached at a comparatively lower water movement intensity.

The present study has also shown that the diffusional effects of water movement can counteract the damaging effects of light intensity. In the field, this interaction was best illustrated by the horizontal distribution of *P. capillacea*, which tolerates full sunlight only when exposed to very high levels of water movement. In the laboratory, high water movement, high water renewal rates, or addition of nutrients allowed all three species (within their individual limits) to utilize more efficiently higher levels of light and temperature, as shown by the absence of bleaching and by faster growth.

The seasonal changes of biomass and dis-

tribution of both species of *Pterocladia* in Hawaii are better explained by this water movement–light intensity interaction than by temperature changes, as has been previously reported in the literature for other Gelidiales. During winter months both species of *Pterocladia* extended their horizontal distribution on the reef in close correlation with the horizontal increases of water movement on the reef and the general decrease of light intensity that occurs in Hawaii. After winter, as light intensity increases and water movement decreases, thallus bleaching increases, thallus size decreases, and both species become restricted to the proximity of their respective reef margins. In *P. caerulescens* there is evidence that apical decay after spore release also plays a role in reducing thallus length (Santelices 1978). The biomass of *G. acerosa* also changes seasonally, but the species appears and disappears in a somewhat random manner across the reef. These thalli live entangled beneath or mixed with other frondose algae that can locally modify the net effects of the seasonally changing values of light and water movement. In addition, they are more sensitive to mechanical stress than the two species of *Pterocladia* (Santelices 1976*a*). Therefore, intense water movement such as that measured at Hauula during November results in decreased harvestable biomass the month after.

The light intensity–water movement interaction is likely to be complex in nature due to the modifying effects of temperature and nutrients. Thus, the experimental results on the Hawaiian Gelidiales indicate that the bleaching effects of light intensity are increased at high temperature while the counteracting effects of water movement can be supplemented or replaced by the addition of nutrients. Summer bleaching has already been attributed (Yamada and Iwahashi 1964) to a deficiency of nitrogen in the seawater due to active metabolism of this element induced by high water temperatures and brighter sunlight. The present results are consistent with this idea but indicate that water movement should be incorporated as a factor increasing fertilizer availability. This multiple interaction probably has major ecological importance as a general explanation for the spatial and temporal distribution of the most common Hawaiian Gelidiales and perhaps of other red algae. It also perhaps explains the bleaching of Gelidiales commonly reported from the upper intertidal levels. There, values for temperature and sunlight are known to be higher, while diffusion enhancement values are lower than in the subtidal.

ACKNOWLEDGMENTS

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